Maternal effects as a mechanism for manipulating male care and resolving sexual conflict over care

Maternal effects as a mechanism for manipulating male care and resolving sexual conflict over care

Matthieu Paquet and Per T. Smiseth

Institute of Evolutionary Biology, School of Biological Sciences, The University of Edinburgh, Charlotte Auerbach Road, Edinburgh, EH9 3FL, UK

Address correspondence to M. Paquet. Email: matthieu.paquet@outlook.com

Manuscript information:

Abstract: 250 words; Main text: 7138 words; 113 references, 1 table, 3 figures

Abstract

Understanding how sexual conflict influences male and female parental decisions is a long-standing problem in behavioral ecology. Until now, most research on sexual conflict over parental care has focused on behavioral mechanisms mediating the resolution of this conflict through negotiation between parents. Here, we review evidence suggesting that maternal effects that alter offspring phenotypes may provide females with a mechanism for manipulating male care. We show that empirical studies on the role of maternal androgens in birds with biparental care provide no support for female manipulation of male care. However, we argue that it would be premature to conclude that maternal androgens play no role in female manipulation of male care given methodological problems in previous work. We then identify a number of additional mechanisms by which females may manipulate male care, including egg components other than androgens, egg size and egg coloration. We show that there is good evidence that egg coloration affects male care, suggesting that this mechanism warrants further research. We also highlight that current evidence is derived from studies using experimental design that target specific candidate mechanisms, such as maternal androgens. Given the multitude of candidate mechanisms, we discuss an alternative approach based on targeting ecologically relevant pre-natal conditions, such as food availability, and monitoring subsequent effects on candidate mechanisms, offspring phenotypes, and male and female care. Finally, we argue that it is timely to extend this work beyond birds with biparental care to include other taxa and species with uniparental male care and cooperative breeding.

Key words: begging, biparental care, egg coloration, egg size, female care, male care, manipulation, maternal androgens, sexual conflict

INTRODUCTION

Understanding how sexual conflict shapes the evolution of male and female parental strategies is a fundamental and long-standing problem in behavioral ecology (Clutton-Brock, 1991; Royle et al., 2012; Trivers, 1974). In the context of parental care, sexual conflict arises because the benefits of care to the offspring are due to the combined effort of the two parents, while the costs of care to each parent are due to its own personal effort. As a consequence of this, each parent should be under selection to minimize its personal effort by shifting as much as possible of the workload over to its partner (Houston et al., 2005). Thus, sexual conflict poses an important theoretical problem because it undermines the evolutionary stability of biparental care. Given this problem, most research into sexual conflict over parental care has focused on identifying behavioral mechanisms that mediate the resolution of this conflict, thereby allowing biparental care to remain evolutionarily stable (Harrison et al., 2009; Houston et al., 2005; Lessells and McNamara, 2012).

Theoretical models have identified three behavioral mechanisms that may mediate the resolution of sexual conflict over parental care (Lessells 2012; Lessells and McNamara, 2012): negotiation, matching and sealed-bid responses. Negotiation occurs when each parent adjusts its level of care in direct response to its partner's contribution, such that the focal parent partially compensates for a reduction in amount of care provided by its partner (McNamara et al., 1999). Matching occurs when each parent adjusts its level of care to its partner's contribution by matching any increase or reduction in its partner's contribution (Johnstone and Hinde, 2006). Finally, sealed bids models assume that each parent makes an initial fixed decision about how much care to provide that is independent of its partner's decision (Houston and Davies, 1985). Although a meta-analysis of work on birds provides overwhelming support for negotiation models (Harrison et al., 2009), there is empirical support for all three models (e.g. Hinde, 2006; Schwagmeyer et al., 2002; Wright and Cuthill,

1989). In models of negotiation, matching or sealed-bid, the two parents use similar behavioral strategies to influence the amount of care provided by their partner after the hatching of their offspring, suggesting symmetry between male and female parents with respect to how much influence they have on the resolution of sexual conflict. However, there is mounting evidence that female birds can adjust the levels of hormones or other egg components that influence offspring behavior or development in response to environmental cues (Meylan et al., 2012; Saino et al., 2002; Von Engelhardt and Groothuis, 2011). Such maternal effects may induce asymmetry between the sexes by providing females with a mechanism for manipulating male contributions towards parental care by altering offspring behavior or development (Moreno-Rueda, 2007; Müller et al., 2007). Maternal effects would allow females to influence male care without the need to interact with the male partner while he provides care, suggesting that maternal effects may be as relevant to species with uniparental male care as to species with biparental care. Therefore, an important yet unresolved issue in this field is whether females exercise greater control over the resolution of sexual conflict via maternal effects (Moreno-Rueda, 2007; Müller et al., 2007).

The aim of this review is first to provide a brief overview over male involvement in parental care and sexual conflict over the male's involvement in care, and then discuss different maternal effects mechanisms by which females may influence male care. We highlight that relatively few empirical studies have directly investigated female manipulation in the context of sexual conflict. All of these studies were focused on testing the manipulating androgens hypothesis (MAH) in birds with biparental care. The MAH focuses on the mechanistic basis of female manipulation of male care in birds, and suggests that females deposit androgens into the eggs in order to stimulate offspring begging, thereby elevating the level of male care. We discuss potential methodological issues arising from previous empirical tests of the MAH. We then identify a number of alternative mechanisms to

androgens, including other egg components, egg size and egg coloration, and suggest that the results from studies on some of these mechanisms are consistent with female manipulation of male care. Considering that females could use any one of these mechanisms to manipulate male care, we propose another approach to test for female manipulation of male care that is independent of the mechanistic basis of such manipulation. This approach would involve the experimental manipulation of ecologically relevant pre-natal conditions (i.e., conditions that are expected to trigger facultative changes in maternal effects), and the monitoring of subsequent effects on candidate mechanisms, offspring phenotypes and male and female parental effort. Finally, we argue that it is timely to expand work beyond the current focus on birds with biparental care to include other animal taxa and species with uniparental male care and cooperative breeding.

MALE CARE AND SEXUAL CONFLICT

Given that maternal effects can only influence the outcome of sexual conflict over parental care if males contribute towards parental care, we start by providing a brief overview of the taxonomic distribution and diversity of male involvement in parental care. Although male parental care is relatively rare compared to female care, male care has evolved repeatedly across a wide range of animal taxa, including birds, mammals, amphibians, fishes, arthropods and annelids (Ridley, 1978; Royle et al., 2012). As hinted at earlier, male care occurs in two distinct contexts: biparental care where the male cooperates with the female in providing care for their joint offspring, and uniparental male care where the male is the sole care-giver. Biparental care is common in birds (Cockburn, 2006), but it also occurs in a small number of mammals, fishes, amphibians and arthropods (Balshine, 2012; Trumbo, 2012). Meanwhile, uniparental male care is relatively common in fishes and amphibians (Balshine, 2012; Gross and Sargent, 1985), and also occurs in some arthropods, such as sea spiders, assassin bugs and

giant waterbugs (Tallamy, 2001). Biparental care tends to involve elaborate forms of care, such as progressive provisioning where parents repeatedly provide the offspring with food after hatching and offspring often beg for food from the parents (Royle et al., 2012). In contrast, uniparental male care tends to involve relatively simple forms of care, such as guarding of eggs or juveniles. In species with uniparental male care and biparental care, maternal effects provide one mechanism by which females could influence the resolution of sexual conflict over parental care. Meanwhile, in species with biparental care, females could influence male care via a combination of maternal effects prior to hatching or birth and behavioral mechanisms such as negotiation and matching after hatching or birth. Thus, in species with biparental care, the role of negotiation between the two parents after hatching may depend on the extent to which male care is influenced by maternal effects on offspring phenotypes.

In behavioral ecology, relatively simple cost-benefit analyses are used to derive the optimal amount of male (and female) care (Fig. 1). The benefits of care are typically measured in terms of enhanced offspring fitness (i.e. offspring survival and/or growth), and the indirect benefits to the male parent can be calculated as the increase in offspring fitness that is due to male care multiplied by the coefficient of relatedness between the male and the offspring. Thus, one factor that may induce variation in the benefits of male care is losses in paternity, which influences the coefficient of relatedness between the male and the offspring. The costs of parental care, on the other hand, are measured in terms of reduced personal fitness (i.e., current and future mating opportunities and/or future survival and reproductive success). Loss of mating opportunities is an important cost of parental care to males in many species given that parental care in general is a mutually exclusive activity with the pursuit of additional mates (Alonzo, 2012; Houston and McNamara, 2002; Kokko and Jennions, 2008).

Models of parental care typically assume that the benefit function to the offspring increases at a decelerating rate to reach an asymptote, while the cost function to the parent increases either linearly or at an accelerating rate (Kilner and Hinde, 2012; Lessells and McNamara, 2012). In either case, the optimal amount of male care is found by identifying the level of care that maximizes the net balance between the indirect benefits and the direct costs of care (Fig. 1). It is important to recognize that this level corresponds to the optimal amount of male care from the male's own perspective. To find the optimal amount of male care from the female's perspective, we need to recognize that the female gains the same indirect benefits from male care as the male, but that she incurs no costs from the male's effort (unless she pairs with the male for life). Thus, the optimum from the female's perspective is for the male to provide the maximum amount of care (Fig. 1; Lessells and McNamara, 2012). In this simple model, sexual conflict is represented as the divergence in the optimal amount of male care between males and females. The actual amount of care that the male provides is determined by the resolution of this conflict, which in turn depends on whether the female somehow can influence the male's decision about how much care to provide. In the next section, we will discuss how maternal effects might influence male care either by biasing the amount of male care away from the male's optimum and towards her own optimum, or by altering the benefit and/or cost functions of parental care to the male.

MATERNAL EFFECTS AND RESOLUTION OF SEXUAL CONFLICT

Maternal effects have received growing attention as important mechanisms that can promote adaptation in complex and changing environments (Groothuis et al., 2005; Meylan et al., 2012; Mousseau and Fox, 1998). Maternal effects can broadly be described as the causal effect of the female's phenotype on the phenotype of the developing offspring over and above the direct effects of genes that the offspring inherit from their mother (Mousseau and Fox,

1998). When adaptive, maternal effects are expected to influence the offspring's phenotype in a way that maximize either the offspring's fitness (i.e. anticipatory maternal effects; Marshall and Uller, 2007) or the mother's own fitness (i.e. selfish maternal effects; Marshall and Uller, 2007). Such adaptive maternal effects can be mediated through a wide range of epigenetic mechanisms. For example in oviparous species, females might adjust the offspring's phenotype through a variety of egg components, such as nutrients (e.g. proteins, lipids and carotenoids), or hormones (e.g. androgens and corticosterone) (Badyaev, 2008; Von Engelhardt and Groothuis, 2011). If the environmental conditions prior to breeding predict the conditions that the offspring are likely to encounter after hatching, the mother could adjust the offspring's development based on cues from the pre-natal environment to match the offspring's phenotype to the post-hatching conditions before the offspring have developed their own ability to do so (Burgess and Marshall, 2014). As predicted, several studies have demonstrated adjustments in maternal effects to various pre-natal environmental conditions, such as food availability or mate quality (Benton et al., 2005; Sheldon, 2000). For example, in barn swallows (*Hirundo rustica*) and zebra finches (*Taeniopygia guttata*), females deposit more androgens in eggs when they are mated with attractive males (Gil et al., 1999; Gil et al., 2006).

Maternal effects may play a role in the resolution of sexual conflict over parental care by providing females with a potential mechanism for influencing male care through adjustments of the offspring's phenotype. Maternal effects may influence the male's decision on how much care to provide by changing the offspring's phenotype, thereby altering the benefits and/or costs of parental care. For example, males often adjust the amount of care they provide in response to the offspring's phenotype, such as the offspring's size (Smiseth et al., 1998) and/or begging behavior (MacGregor and Cockburn, 2002; Müller et al., 2007; Smiseth and Moore, 2004), presumably because these cues provide males with information on the

benefits of continued parental care. In this context, females would be under selection to adjust the offspring's phenotype such that it extracts as much care as possible from the male, thereby shifting more of the costs of care towards the male. Whether such maternal effects should increase offspring fitness (anticipatory maternal effects) and/or female fitness (selfish maternal effects) depends on whether the increase in male care is offset by a corresponding decrease in female care, and the extent to which any decrease in female care increases the female's future reproductive potential (Marshall and Uller, 2007). For example, if females are under selection to invest in current reproduction, females might maintain their level of care in response to an increase in male care. In this situation, we would expect maternal effects to improve offspring rather than female fitness. On the other hand, if females are under selection to favor investment in future reproduction, females might respond to an increase in male care by reducing their level of care. Thus, in this situation, we would expect maternal effects to improve female rather than offspring fitness. In light of this argument, we suggest that the extent to which maternal effects should increase offspring and/or female fitness may depend on the life history of the species (Marshall and Uller, 2007; Stearns, 1992).

So far, we have discussed female manipulation of male care without defining what we mean by the term 'manipulation'. We define female manipulation as the outcome of any mechanism used by the female to influence the amount of care provided by her male partner in a way that increases the female's and/or offspring's fitness at the expense of the male's fitness. We assign fitness following Smiseth et al. (2012) such that offspring survival from egg formation is assigned as part of the offspring's direct fitness. Although there are other definitions of manipulation, the definition provided above is consistent with previous definitions as one individual altering the behaviour of another against the best interests of the latter (eg. Dawkins, 1999). Based on the cost-benefit analysis introduced earlier, it is possible to distinguish between two forms of female manipulation: (1) deception, which occurs when

maternal effects somehow bias the amount of care provided by the male away from the male's optimum and towards the female's own optimum (Fig. 2a), and (2) incentivization, which occurs when maternal effects somehow modify the benefit and/or cost functions of care such that it increases the male's optimal amount of care (Fig. 2b-c). The distinction between these two forms of manipulation is significant because they are likely to differ with respect to their evolutionary stability. Deception is likely to be evolutionarily unstable because the male should be under selection to evolve counter-strategies that help re-store his optimum. For example, if females deposit compounds into the eggs that stimulate begging offspring to exaggerate their true needs, males could simply respond over evolutionary time by becoming progressively less responsive to offspring begging. Theoretical considerations suggest that, although deceptive manipulation may be evolutionary unstable, it might nevertheless drive subsequent evolutionary changes in parental care. As shown in a recent theoretical study, if there is a slight difference in the costs and/or benefits of care to males and females, the sex with the lower costs or higher benefits of care will evolve to become both more able to provide care and to provide much higher levels of care than the other sex (McNamara and Wolf, 2015). Thus, deception might drive the evolution of stable sex differences in parental care strategies by inducing slight initial differences in the costs and/or benefits of care between male and female parents.

Incentivization, on the other hand, is likely to be evolutionarily stable because, with this form of manipulation, maternal effects induces changes in benefit and/or cost functions of parental care, thereby altering the amount of care that is optimal from the male's perspective. For example, if females reduce their initial investment in eggs such that the offspring require an increase in the amount of post-hatching parental care, males should respond by increasing their contribution towards parental care due to the corresponding shift in the benefit function of care. The difference between deception and incentivization is that the male provides more

237 care than is optimal to the male in the former case while the male provides the optimal
238 amount of given the current circumstances determined by maternal effects in the latter care.
239 Below, we provide an overview of possible mechanisms by which females might manipulate
240 male care.
241
242 **HOW CAN FEMALES MANIPULATE MALE CARE?**
243 As stated earlier, maternal effects might provide females with a means for manipulating male
244 care through a number of different mechanisms, such as hormones (e.g. androgens and
245 corticosteroids), or nutrients (e.g. proteins, lipids, carotenoids Badyaev, 2008). Until now, the
246 study of female manipulation of male care has been intimately linked to the mechanistic basis
247 of such manipulation. The reason for this is that the original hypothesis, known as the
248 manipulating androgens hypothesis (MAH), focused on androgens as the specific mechanism
249 by which female birds may manipulate male care. In this section, we will start by discussing
250 the logic of the MAH before reviewing empirical evidence for potential effects of maternal
251 androgens on male care. Given that the general logic of the MAH applies to any mechanism
252 females potentially could use to manipulate male, we then review evidence suggesting that
253 these mechanisms could allow females to manipulate male care.
254
255 **Manipulating androgens**
256 The manipulating androgens hypothesis (MAH) is a verbal hypothesis proposing that female
257 birds can manipulate male care by depositing androgens such as testosterone in the eggs,
258 thereby stimulating offspring begging and ultimately increasing the male's contribution
259 towards food provisioning (Moreno-Rueda, 2007; Müller et al., 2007). The MAH was
260 proposed against a background of growing evidence that female birds deposit androgens into
261 their eggs (Gil et al., 2007; Schwabl, 1996), and that females can adjust how much androgens

they deposit into their eggs in response to pre-natal cues that predict the environmental conditions the offspring would experience after hatching (Mazuc et al., 2003; Sandell et al., 2007; Von Engelhardt and Groothuis, 2011). Furthermore, there was also growing evidence that maternal androgens stimulate offspring begging (Schwabl, 1996; Smiseth et al., 2011; Von Engelhardt and Groothuis, 2011). Thus, the MAH suggests that females deposit androgens in the eggs as a mechanism for manipulating male care, given that their effects on offspring begging could be used to extract more care from the male. However, for this to be possible, it is essential for female manipulation of offspring begging to have a differential impact on the costs of care for males and females. For this to be the case, males must be more responsive to an increase in offspring begging than females (Moreno-Rueda, 2007). There is some evidence that this requirement is met, as studies on some birds and insects show that males respond more strongly to an increase in nestling begging (MacGregor and Cockburn, 2002; Müller et al., 2007; Smiseth and Moore, 2004).

Currently, six experimental studies have tested the MAH, all of which have been conducted on birds with biparental care (Table 1). Four studies tested the MAH by experimentally elevating levels of yolk androgen, one injected flutamide (an androgen blocking agent) in the eggs, and one measured testosterone levels of the fourth egg and cross-fostered the remaining clutch (Table 1). All studies monitored subsequent effects of these experimental treatments on offspring begging and/or male food provisioning (Table 1). None of these studies found any evidence for a causal effect of yolk androgen levels on male parental effort. In fact, one study found evidence that contradicts the MAH, as only female great tits (*Parus major*) reduced their food provisioning towards enlarged broods when an androgen-blocking agent was injected to the eggs (Tschirren and Richner, 2008). The only study to report some evidence in support of the MAH found that injection of testosterone into the eggs of yellow-legged gulls (*Larus michahellis*) increased a component of nestling

287 begging (i.e., chatter calls) that was more strongly correlated with male provisioning rates
288 than with female ones (Noguera et al., 2013). However, given that this study did not directly
289 test for a causal effect of the manipulation of testosterone on the provisioning of the two
290 parents, this evidence should be interpreted with care.

291 As outlined above, there is no clear-cut evidence in support of the MAH, suggesting
292 that we perhaps should reject the hypothesis. However, such a conclusion would be premature
293 given that the lack of evidence in support of the MAH could be due to methodological
294 shortcomings with the previous experiments. For example, previous studies of the MAH
295 recorded the effects of elevated levels of maternal testosterone on parental provisioning rates
296 after the stage in the nestling's development when maternal testosterone has its strongest
297 effect on nestling begging. Previous work suggests that maternal effects on nestling begging
298 may be more pronounced during the first few days after hatching (Schwabl, 1996). However,
299 all studies that investigated the effect of testosterone on male parental effort recorded effects
300 on male provisioning rates 5–10 days after hatching (Table 1). For example, in the study on
301 house wrens (*Troglodytes aedon*), maternal testosterone was found to affect nestling begging
302 on days 4–5 after hatching but not on days 9–10 after hatching (Barnett et al., 2011).
303 Nevertheless, this study tested for effects of maternal testosterone on male provisioning rates
304 on days 9–10 after hatching (Barnett et al., 2011), when the potential effects of maternal
305 testosterone on begging no longer appear. Thus, further work on birds is needed to test the
306 MAH, and such work should now ensure that any effects on male care are measured during
307 the first few days after hatching.

308 A second potential methodological issue is that these studies focused on one specific
309 mechanism: the effect of maternal androgens on offspring begging. The historical emphasis
310 on maternal androgens as the focal mechanism by which females can manipulate male care is
311 understandable in light of the early discovery that female birds deposit testosterone into eggs.

However, the basic logic of the MAH applies to any maternal effect that females can adjust in response to pre-natal cues predicting the environmental conditions the offspring are likely to experience, and that might influence male care through its effect on the offspring's phenotype. Thus, in the following parts of this section, we discuss evidence suggesting that other such maternal effects might provide females with a means for manipulating male care.

Other egg components

There is mounting evidence that females deposit a wide range of compounds into their eggs, some of which are known to influence nestling begging. For example, female birds deposit several non-androgen hormones, including corticosteroids, into their eggs (Smiseth et al., 2011; Von Engelhardt and Groothuis, 2011). There is evidence that females adjust the deposition of corticosteroids in response to pre-natal environmental variations (Meylan et al., 2012). For example, studies on tree-spined sticklebacks (*Gasterosteus aculeatus*) (Giesing et al., 2011), Japanese quails (*Coturnix japonica*) (Hayward et al., 2005) and barn swallows (Saino et al., 2005) show that females deposit more corticosteroids in their eggs when they are exposed to more stressful pre-natal conditions. However, existing evidence suggests that elevated levels of maternal corticosteroids have a detrimental effect on the offspring (Von Engelhardt and Groothuis, 2011). For example, a study on the tropical damselfish *Pomacentrus amboinensis* show that maternal cortisol reduces the body size of fry at hatching (McCormick, 1998).Furthermore, in yellow-legged gulls elevated maternal corticosterone suppresses nestling begging and growth (Rubolini et al., 2005). Thus, given that corticosteroids seem to suppress offspring growth and development, it seems unlikely that females could manipulate male care by elevating the levels of these hormones.

Insects have a hormone system that is quite different from that of vertebrates (Nijhout, 1998). Nevertheless, there is evidence suggesting that female insects also deposit hormones in

337 their eggs (De Loof et al., 2013). For example, many insects, including the silkmoth *Bombyx*
338 *mori*, produce eggs that are rich in ecdysteroids and juvenile hormones (Gharib and de Reggi,
339 1983). Ecdysteroids and juvenile hormones are involved in the regulation of numerous aspects
340 of insect development, physiology, and behavior (Nijhout, 1998). It is currently unknown
341 whether female insects adjust the deposition of ecdysteroids or juvenile hormones based on
342 pre-natal environmental cues. Nevertheless, there is some evidence that elevated juvenile
343 hormone levels can stimulate larval begging in the burying beetle *Nicrophorus vespilloides*
344 (Crook et al., 2008). In this and other species of the genus *Nicrophorus*, males often assist the
345 female during breeding by providing care for the developing larvae, suggesting that females
346 potentially could deposit juvenile hormones into the eggs as a mechanism for manipulating
347 male involvement in care. Thus, further work is now needed to examine the role of juvenile
348 hormones and ecdysteroids as mechanisms for manipulating male care in these beetles and
349 other insects with biparental care or uniparental male care.

350 Females also deposit various non-hormonal compounds into their eggs, including
351 carotenoids. Carotenoids are fat-soluble pigments (von Schantz et al., 1999) that are
352 exclusively obtained from the diet, and the amount of carotenoids in the diet may therefore
353 reliably reflect food availability prior to breeding (Blount et al., 2000). There is evidence from
354 studies on birds that maternal deposition of carotenoids varies with pre-natal conditions as
355 females of several species increase their deposition of carotenoids in egg yolk when
356 supplemented with a carotenoid-rich diet (Berthouly et al., 2007; Ewen et al., 2008; McGraw
357 et al., 2005). Such an increase in yolk carotenoids often result in higher phenotypic quality of
358 the offspring (Berthouly et al., 2007; Biard et al., 2005; Marri and Richner, 2014).
359 Furthermore, carotenoids are known to stimulate begging intensity in great tits (Helfenstein et
360 al., 2008) and affect the nestling's mouth coloration in hihis (*Notiomystis cincta*) (Thorogood
361 et al., 2008). Thus, given that carotenoids stimulate offspring growth and begging, it is

362 possible that females could deposit carotenoids into their eggs to manipulate male care. Thus,
363 there is now a need for further work to examine whether maternal carotenoids might influence
364 the amount of care provided by the male (Dugas, 2015).
365
366 **Egg size**
367 Egg size is often used as a proxy for the amount of energy and nutrients that female parents
368 invest into each egg (Bernardo, 1996; Christians, 2002). There is evidence that females adjust
369 egg size depending on the environmental conditions, as experimental studies on insects,
370 amphibians or fishes have found that females increase egg size under more stressful
371 environmental conditions (Fox et al., 1997; Kaplan, 1992; Taborsky, 2006; Vijendravarma et
372 al., 2010). For example, in cooperative breeding species, there is evidence that females lay
373 smaller eggs as the number of helpers increases, as has been reported for several bird species
374 (Canestrari et al., 2011; Paquet et al., 2013; Russell et al., 2007; Santos and Macedo, 2011)
375 and as well for one fish species (Taborsky et al., 2007). This adjustment in egg size suggests
376 that the females reduce their investment in eggs in response to predictable cues about the
377 number of helpers that would provide care for the offspring. As predicted by a recent game-
378 theoretical model, females might reduce egg size if an increase in post-hatching care by the
379 parents and their helpers can compensate for the effects of the reduction in egg size (Savage et
380 al., 2015). Although this model applies to cooperatively breeding species, its logic may apply
381 to species with biparental care or uniparental male care by substituting the number of helpers
382 with the male's ability to provide post-hatching care. Thus, there is now a need for studies
383 investigating whether females may adjust egg size in response to cues about the male's ability
384 to provide care in species with biparental care or uniparental male care.
385 A reduction in egg size by females may influence the amount of male care indirectly
386 by stimulating the offspring's begging behavior, as described above for the MAH. For

example, given smaller eggs may hatch offspring with lower energy reserves (Christians, 2002; Krist 2011), offspring hatching from smaller eggs may beg at higher levels because they have higher hunger levels. We are unaware of any previous work investigating effects of egg size on offspring begging. Thus, further work is needed to test for effects of egg size on offspring begging. Potentially males may visually assess egg size during the egg stage, in which case males may adjust the amount of care they provide in direct response to egg size rather than its potential effects on offspring begging. Males may be expected to adjust the amount of care they provide in response to egg size given that egg size is strongly correlated with offspring condition early after hatching (Christians, 2002). Smaller eggs often hatch into offspring with lower energy reserves and lower survival prospects, especially under adverse environmental conditions (Benton and Grant, 1999; Fox et al., 1997). Thus, a reduction in egg size might alter the benefit function of male care given that parental care is thought to have evolved to enhance offspring fitness by buffering adverse environmental conditions (Royle et al., 2012). If so, a reduction in egg size might be expected to alter the benefit function of care, thereby creating an incentive for males to increase their contribution towards care.

Currently, little is known about the causal effect of egg size on the amount of care provided by males. For example, if the negative effects of a reduction in egg size can be compensated by post-natal parental care (i.e. "head start" hypothesis sensu Savage et al., 2015), we would expect a negative correlation between eggs size and the amount of male care. There is no evidence that this is the case from the few studies that directly investigated the relationship between egg size and parental care in birds with biparental care (Krist, 2009; Quillfeldt and Peter, 2000). However, it is important to note that these studies did not test for sex-specific effects of egg size on parental care, and that it is therefore possible that egg size is negatively correlated with male care but positively correlated with female care. Thus, there is now need for experimental studies specifically designed to test for effects of egg size on

male and female care. It may appear challenging to disentangle between adjustments in egg size as a female strategy specifically used to manipulate male care and adjustments in egg size as a general female life history strategy that is independent of male manipulation. However, evidence that adjustments of egg size are associated with a decrease in male fitness and an increase in female and/or offspring fitness would support the hypothesis that females adjust egg size to manipulate male care. Additionally, in species where egg size *per se* influences male care, it would be possible to experimentally test whether egg size provides females with a means to manipulate male care by providing parents with different-sized dummy eggs and monitor subsequent effects on male contributions towards care.

Egg coloration

Egg coloration may not seem an obvious mechanism for female manipulation of male care. However, there is growing evidence that variation in egg coloration affects male care in some birds with biparental care (Moreno et al., 2006b; Sanz and García-Navas, 2009; Soler et al., 2005), suggesting that egg coloration may provide females with a mechanism for manipulating male care. The evolution of egg coloration in birds has received considerable attention given its diversity both between and within species (Kilner, 2006; Underwood and Sealy, 2002). The sexually selected egg color hypothesis (SSEC) suggests that the blue-green pigmentation of avian eggs, which is caused by the antioxidant biliverdin, may act as a post-mating sexual signal that communicates the female's condition or genetic quality to the male (Moreno and Osorno, 2003). Studies on pied flycatchers (*Ficedula hypoleuca*) and spotless starlings (*Sturnus unicolor*) show that experimental manipulation of the female's condition influences the blue-green coloration of the eggs (Moreno et al., 2006a; Soler et al., 2008). The SSEC suggests that males gain a fitness benefit by adjusting their investment in response to variation in egg coloration, because egg coloration reflects female's genetic quality and/or

condition. If so, males may increase the amount of care they provide when females lay eggs that are more pigmented because the offspring of better mates would merit more parental effort according to the differential allocation hypothesis (Moreno and Osorno, 2003).

In support of the SSEC, several studies have found evidence for a positive effect of egg coloration on male care (Moreno et al., 2006b; Sanz and García-Navas, 2009; Soler et al., 2005 but see Krist and Grim, 2007; Stoddard et al., 2012). It is noteworthy that experimental manipulation of egg coloration had a significant positive effect on male but not female provisioning rates in spotless starlings (Soler et al., 2008), American robins (*Turdus migratorius*) (English and Montgomerie, 2011) and house wrens (Walters et al., 2014). Given that egg coloration seems to influence male care only, females could use this mechanism as a means for manipulating male care. Although these results on the effects of egg coloration on male have not traditionally been interpreted as evidence for female manipulation of care, current evidence suggest that egg coloration is the most promising mechanism by which females might manipulate male care. To confirm that egg coloration provides a mechanism for female manipulation of male care, we need further studies that investigate the fitness consequences of egg coloration for males and females. If egg coloration is used as a mechanism for female manipulation of male care, we would expect egg coloration to enhance the female's current or future reproductive potential at the expense of the male's future reproductive potential.

Other mechanisms

Above, we have reviewed some of the most likely mechanisms females could use to manipulate male care based on information in the published literature. However, it is possible that females could use a variety of other egg characteristics providing (1) that females can adjust this characteristic in response to pre-natal conditions, (2) that it affects an aspect of the

offspring's phenotype that the male can access, and (3) that the male adjust his level of care in response to this trait. For example, in many fishes with male care, males often cannibalize some of the eggs to lower their energetic costs of care (Klug and Bonsall, 2007; Manica, 2002). If so, females could potentially modify some eggs properties that increase the cost of cannibalism to the males, thereby increasing the offspring's fitness at the expense of the male's own fitness. In support of this suggestion, the evolution of care in harvestmen seem to coincide with mucus or attachment of debris on the surface of the eggs, possibly representing an adaptation whereby females can reduce male cannibalism (Requena et al., 2009). Furthermore, in an assassin bug species with male care, the eggs are darker compared with an ecologically similar species with female care, which may reflect that the former have a thicker egg wall to increase the costs of male egg cannibalism (Gilbert et al., 2010).

FUTURE RESEARCH DIRECTIONS

Mechanisms versus maternal effects?

As discussed above, previous experimental work on female manipulation of male care have focused on the MAH, and have tested this hypothesis by manipulating the level of androgen in the eggs and monitoring subsequent effects on offspring begging and/or male care (Table 1). The advantage of this experimental approach is that it is explicit about the specific mechanism by which females might manipulate male care. However, an obvious disadvantage of this experimental approach is that females might manipulate male care through a different mechanism than the one that was targeted in the experimental manipulation, including other compounds deposited into eggs, egg size and egg coloration. One potential solution to this problem is to repeat the experiment such that it targets every possible mechanism that could be used by females. However, this strategy is likely to be labor-intensive and may remain

inconclusive as females might manipulate male care through a mechanism that is yet to be discovered.

An alternative approach to the one used hitherto is to consider the ecological context of the maternal effects that females are expected to use as a means to manipulate male care. Thus, rather than targeting a specific candidate mechanism, experiments could target some aspect of the pre-natal environmental conditions and then monitor subsequent effects on male and female parental care and male, female and offspring fitness (Fig. 3). For example, if females and/or offspring benefit from higher levels of male care when food availability is low, we might expect females to adjust some unknown maternal effect in response to food availability, with subsequent effects on the offspring's phenotype (e.g., offspring begging) and the amount of male care. The strength of this approach is that it is independent of the specific mechanism by which females manipulate male parental care. Thus, this approach reduces the risk of incorrectly rejecting female manipulation due to not targeting the correct mechanism and would even work in systems where there is no prior information on potential candidate mechanisms.

A potential weakness of this approach is that, in order to demonstrate effects on male and female parental care due to the pre-natal environmental conditions, it is important to exclude potential effects due the post-natal environmental conditions. Separating these effects is essential because the pre-natal conditions might correlate with the post-natal conditions, and the effects of the pre-natal conditions mediated through maternal effects on the eggs are likely to be weaker than the effects of the post-natal conditions on the level of parental care after hatching (Krist, 2011). In order to overcome this problem, it is therefore essential to implement cross-fostering experiments within this approach. Such cross-fostering experiments would allow us to disentangle the effects of the pre-natal environmental conditions on male and female parental care from those of the post-natal environmental

conditions (see for example Hinde et al., 2009; Paquet et al., 2015). Another disadvantage of this approach is that it provides no information on the mechanism by which females manipulate male care. This problem could be addressed by testing between possible candidate mechanisms once maternal manipulation of male care has been documented. This could be done based on the same experimental design as described above, but by monitoring subsequent effects on a wide range of possible candidate mechanisms. Once candidate mechanisms have been identified, experiments should be conducted that specifically target each candidate mechanism.

Beyond biparental care

Until now, female manipulation of male care has only been considered for birds with biparental care. However, given that maternal effects are mediated through the offspring's phenotype, they provide females with a mechanism for manipulating male care even if females do not interact with the male while he provides care. Thus, maternal effects may be as important in species with uniparental male care as in species with biparental care. Indeed, species with uniparental male care might be better suited as models for studying female manipulation of male care because its role in the resolution of sexual conflict is not confounded by effects due to other mechanisms of conflict resolution, such as negotiation or matching. For example, many fishes might be very well suited as study systems to test for female manipulation of male care in species with uniparental male care (Gross and Sargent, 1985).

Finally, we note that female manipulation also might occur in cooperatively breeding species, where females gain help to raise their offspring from both their male partner and a variable number of helpers. Helpers are non-breeding individuals that assist the breeders by providing care to their offspring, for example by provisioning additional food to the nest

(Brown, 1987; Emlen, 1991). Thus, the presence of helpers represents a predictable improvement in the rearing conditions that females can assess prior to breeding (Fig. 3). There is some evidence that females use the number of helpers as a cue to strategically adjust the size of the eggs that they lay (Russell et al., 2007; Taborsky et al., 2007), or the amount of nutrients (Russell et al., 2007) and hormones (Paquet et al., 2013) deposited into the eggs. In these species, females may manipulate the amount of care provided by both the male and the helpers. Thus, as more than one individual could be manipulated by the breeding females, there is no need for a sex-specific effect on parental effort as any decrease in female care could be overcompensated by an increase in the amount of care provided by the male and the helpers.

In cooperatively breeding species, female manipulation of the amount of care provided by the other group members may also vary with the relatedness between the female and the helpers given that it would be more advantageous for females to manipulate unrelated helpers from an inclusive fitness perspective (Savage et al., 2013). This idea is supported by evidence from previous work on sociable weavers (*Philetairus socius*) showing that offspring beg less when expecting to be fed by more helpers (Paquet et al., 2015). Thus, in this species, the number of helpers in the group co-varies with pre-natal maternal effects on offspring begging. Currently, there are few studies on how parents and helpers respond to changes in offspring begging levels in cooperatively breeding species, but the results obtained so far are consistent with female manipulation of the male and the helpers. For example, in Arabian babblers (*Turdoides squamiceps*), where there is high relatedness within breeding groups, the two parents and the helpers respond in the same way to experimentally manipulated begging (Wright, 1998). On the other hand, in superb fairy-wrens (*Malurus cyaneus*), where the breeding male and the helpers often are unrelated to the brood, the breeding female does not respond to increased begging while the male and the helpers respond by increasing their

feeding rates (MacGregor and Cockburn, 2002). Finally, in sociable weavers adult helpers feed at a higher rate when less related to the breeding female, but not with that of the breeding male (Doutrelant et al., 2011), suggesting that female manipulation is directed towards primarily unrelated helpers. Studying the maternal effect of helpers' number and relatedness to the mother on individual provisioning behavior is thus a promising research avenue to investigate female manipulation in cooperative breeders.

CONCLUSION

Female manipulation of male care has often been assumed to be a rare phenomenon, and its existence has been largely overlooked in the study of sexual conflict over parental care (Lessells and McNamara, 2012). Here, we show that females might use various maternal effects mechanisms for manipulating male care, including androgens deposited into eggs, other egg components, egg size and egg coloration. Given the number of potential mechanisms, we suggest that future work on female manipulation of male care use experimental designs that are independent of the specific underlying mechanism and that they instead focus on the pre-natal conditions that are expected to influence maternal effects, such as food availability.

FUNDING

M.P. was supported by FYSSEN.

ACKNOWLEDGMENTS

We thank Leigh Simmons for inviting us to submit this review as well as two anonymous reviewers for valuable comments on our manuscript.

586 **REFERENCES**

587 Alonzo SH, 2012. Sexual selection favours male parental care, when females can choose.
588 Proc R Soc Lond B 279:1784-1790.
589 Badyaev AV, 2008. Maternal Effects as Generators of Evolutionary Change A Reassessment.
590 Year In Evolutionary Biology 2008 Malden: Wiley-Blackwell. p. 151-161.
591 Balshine S, 2012. Patterns of parental care in vertebrates. The evolution of parental care:62-
592 80.
593 Barnett CA, Clairardin SG, Thompson CF, Sakaluk SK, 2011. Turning a deaf ear: a test of the
594 manipulating androgens hypothesis in house wrens. Anim Behav 81:113-120. doi:
595 10.1016/j.anbehav.2010.09.019.
596 Benton TG, Grant A, 1999. Optimal reproductive effort in stochastic, density-dependent
597 environments. Evolution 53:677-688. doi: 10.2307/2640709.
598 Benton TG, Plaistow SJ, Beckerman AP, Lapsley CT, Littlejohns S, 2005. Changes in
599 maternal investment in eggs can affect population dynamics. Proc R Soc Lond B
600 272:1351-1356.
601 Bernardo J, 1996. The particular maternal effect of propagule size, especially egg size:
602 Patterns, models, quality of evidence and interpretations. Am Zool 36:216-236.
603 Berthouly A, Helfenstein F, Richner H, 2007. Cellular immune response, stress resistance and
604 competitiveness in nestling great tits in relation to maternally transmitted carotenoids.
605 Funct Ecol 21:335-343.
606 Biard C, Surai PF, Moller AP, 2005. Effects of carotenoid availability during laying on
607 reproduction in the blue tit. Oecologia 144:32-44. doi: 10.1007/s00442-005-0048-x.
608 Blount JD, Houston DC, Moller AP, 2000. Why egg yolk is yellow. Trends Ecol Evol 15:47-
609 49. doi: 10.1016/S0169-5347(99)01774-7.

610 Brown JL, 1987. Helping and Communal Breeding in Birds: Ecology and Evolution.
611 Princeton: Princeton University Press.
612 Burgess SC, Marshall DJ, 2014. Adaptive parental effects: the importance of estimating
613 environmental predictability and offspring fitness appropriately. Oikos 123:769-776.
614 Canestrari D, Marcos JM, Baglione V, 2011. Helpers at the nest compensate for reduced
615 maternal investment in egg size in carrion crows. J Evol Biol 24:1870-1878. doi:
616 10.1111/j.1420-9101.2011.02313.x.
617 Christians JK, 2002. Avian egg size: variation within species and inflexibility within
618 individuals. Biol Rev 77:1-26. doi: 10.1017/S1464793101005784.
619 Clutton-Brock TH, 1991. The evolution of parental care: Princeton University Press.
620 Cockburn A, 2006. Prevalence of different modes of parental care in birds. Proc R Soc Lond
621 B 273:1375-1383.
622 Crook TC, Flatt T, Smiseth PT, 2008. Hormonal modulation of larval begging and growth in
623 the burying beetle Nicrophorus vespilloides. Anim Behav 75:71-77. doi:
624 10.1016/j.anbehav.2007.04.009.
625 Dawkins R, 1999. The extended phenotype: The long reach of the gene: Oxford University
626 Press.
627 De Loof A, Boerjan B, Ernst UR, Schoofs L, 2013. The mode of action of juvenile hormone
628 and ecdysone: Towards an epi-endocrinological paradigm? Gen Comp Endocr 188:35-
629 45.
630 Doutrelant C, Dalecky A, Covas R, 2011. Age and relatedness have an interactive effect on
631 the feeding behaviour of helpers in cooperatively breeding sociable weavers.
632 Behaviour 148:1399-1417. doi: 10.1163/000579511x608701.
633 Dugas M, 2015. Commentary: Parental care and the proximate links between maternal effects
634 and offspring fitness. Oecologia 177:1089-1092. doi: 10.1007/s00442-015-3266-x.

635 Emlen ST, 1991. The evolution of cooperative breeding in birds and mammals. In: Krebs JR,
636 Davies NB, editors. Behavioural ecology: an evolutionary approach 3rd ed Oxford:
637 Blackwell Scientific Publications. p. 301-337.
638 English PA, Montgomerie R, 2011. Robin's egg blue: does egg color influence male parental
639 care? Behav Ecol Sociobiol 65:1029-1036.
640 Ewen JG, Thorogood R, Karadas F, Cassey P, 2008. Condition dependence of nestling mouth
641 colour and the effect of supplementing carotenoids on parental behaviour in the hihi
642 (Notiomystis cincta). Oecologia 157:361-368.
643 Fox CW, Thakar MS, Mousseau TA, 1997. Egg size plasticity in a seed beetle: An adaptive
644 maternal effect. Am Nat 149:149-163.
645 Gharib B, de Reggi M, 1983. Changes in ecdysteroid and juvenile hormone levels in
646 developing eggs of Bombyx mori. J Insect Physiol 29:871-876.
647 Giesing ER, Suski CD, Warner RE, Bell AM, 2011. Female sticklebacks transfer information
648 via eggs: effects of maternal experience with predators on offspring. Proc R Soc Lond
649 278:1753-1759.
650 Gil D, Biard C, Lacroix A, Spottiswoode CN, Saino N, Puerta M, Moller AP, 2007. Evolution
651 of yolk androgens in birds: Development, coloniality, and sexual dichromatism. Am
652 Nat 169:802-819. doi: 10.1086/516652.
653 Gil D, Graves J, Hazon N, Wells A, 1999. Male attractiveness and differential testosterone
654 investment in zebra finch eggs. Science 286:126-128.
655 Gil D, Ninni P, Lacroix A, De Lope F, Tirard C, Marzal A, Pape Møller A, 2006. Yolk
656 androgens in the barn swallow (Hirundo rustica): a test of some adaptive hypotheses. J
657 Evol Biol 19:123-131.
658 Gilbert JD, Thomas LK, Manica A, 2010. Quantifying the benefits and costs of parental care
659 in assassin bugs. Ecol Entomol 35:639-651.

660 Groothuis TGG, Muller W, von Engelhardt N, Carere C, Eising C, 2005. Maternal hormones
661 as a tool to adjust offspring phenotype in avian species. Neurosci Biobehav R 29:329-
662 352. doi: 10.1016/j.neubiorev.2004.12.002.
663 Gross MR, Sargent RC, 1985. The evolution of male and female parental care in fishes. Am
664 Zool 25:807-822.
665 Harrison F, Barta Z, Cuthill I, Székely T, 2009. How is sexual conflict over parental care
666 resolved? A meta-analysis. J Evol Biol 22:1800-1812. doi: 10.1111/j.1420-
667 9101.2009.01792.x.
668 Hayward LS, Satterlee DG, Wingfield JC, 2005. Japanese quail selected for high plasma
669 corticosterone response deposit high levels of corticosterone in their eggs. Physiol
670 Biochem Zool 78:1026-1031. doi: 10.1086/432854.
671 Helfenstein F, Berthouly A, Tanner M, Karadas F, Richner H, 2008. Nestling begging
672 intensity and parental effort in relation to prelaying carotenoid availability. Behav
673 Ecol 19:108-115. doi: 10.1093/beheco/arm103.
674 Hinde C, 2006. Negotiation over offspring care?—a positive response to partner-provisioning
675 rate in great tits. Behav Ecol 17:6-12.
676 Hinde CA, Buchanan KL, Kilner RM, 2009. Prenatal environmental effects match offspring
677 begging to parental provisioning. Proc R Soc Lond 276:2787-2794. doi:
678 10.1098/rspb.2009.0375.
679 Houston A, Davies N, 1985. The evolution of cooperation and life history in the Dunnock,
680 Prunella modularis.
681 Houston AI, McNamara JM, 2002. A self–consistent approach to paternity and parental effort.
682 Philosophical Transactions of the Royal Society B: Biological Sciences 357:351-362.
683 Houston AI, Szekely T, McNamara JM, 2005. Conflict between parents over care. Trends
684 Ecol Evol 20:33-38. doi: 10.1016/j.tree.2004.10.008.

685 Johnstone RA, Hinde CA, 2006. Negotiation over offspring care—how should parents
686 respond to each other's efforts? Behav Ecol 17:818-827.
687 Kaplan RH, 1992. Greater Maternal Investment Can Decrease Offspring Survival In The Frog
688 Bombina-Orientalis. Ecology 73:280-288.
689 Kilner R, 2006. The evolution of egg colour and patterning in birds. Biol Rev 81:383-406.
690 Kilner RM, Hinde CA, 2012. Parent–offspring conflict. The evolution of parental care 119.
691 Klug H, Bonsall MB, 2007. When to care for, abandon, or eat your offspring: the evolution of
692 parental care and filial cannibalism. Am Nat 170:886-901.
693 Kokko H, Jennions MD, 2008. Parental investment, sexual selection and sex ratios. J Evol
694 Biol 21:919-948.
695 Kolm N, 2001. Females produce larger eggs for large males in a paternal mouthbrooding fish.
696 Proc R Soc Lond 268:2229-2234. doi: 10.1098/rspb.2001.1792.
697 Krist M, 2009. Short-and long-term effects of egg size and feeding frequency on offspring
698 quality in the collared flycatcher (Ficedula albicollis). J Anim Ecol 78:907-918.
699 Krist M, 2011. Egg size and offspring quality: a meta-analysis in birds. Biol Rev 86:692-716.
700 Krist M, Grim T, 2007. Are blue eggs a sexually selected signal of female collared
701 flycatchers? A cross-fostering experiment. Behav Ecol Sociobiol 61:863-876.
702 Laaksonen T, Adamczyk F, Ahola M, Möstl E, 2011. Yolk hormones and sexual conflict over
703 parental investment in the pied flycatcher. Behavioral Ecology And Sociobiology
704 65:257-264.
705 Lessells CM, McNamara JM, 2012. Sexual conflict over parental investment in repeated
706 bouts: negotiation reduces overall care. Proc R Soc Lond 279:1506-1514. doi:
707 10.1098/rspb.2011.1690.
708 MacGregor NA, Cockburn A, 2002. Sex differences in parental response to begging nestlings
709 in superb fairy-wrens. Anim Behav 63:923-932. doi: 10.1006/anbe.2001.1991.

710 Manica A, 2002. Filial cannibalism in teleost fish. Biol Rev 77:261-277.
711 Marri V, Richner H, 2014. Yolk carotenoids increase fledging success in great tit nestlings.
712 Oecologia 176:371-377.
713 Marshall DJ, Uller T, 2007. When is a maternal effect adaptive? Oikos 116:1957-1963.
714 Mazuc J, Bonneaud C, Chastel O, Sorci G, 2003. Social environment affects female and egg
715 testosterone levels in the house sparrow (Passer domesticus). Ecol Lett 6:1084-1090.
716 doi: 10.1046/j.1461-0248.2003.00535.x.
717 McCormick MI, 1998. Behaviorally induced maternal stress in a fish influences progeny
718 quality by a hormonal mechanism. Ecology 79:1873-1883.
719 McGraw K, Adkins-Regan E, Parker R, 2005. Maternally derived carotenoid pigments affect
720 offspring survival, sex ratio, and sexual attractiveness in a colorful songbird.
721 Naturwissenschaften 92:375-380.
722 McNamara JM, Gasson CE, Houston AI, 1999. Incorporating rules for responding into
723 evolutionary games. Nature 401:368-371.
724 McNamara JM, Wolf M, 2015. Sexual conflict over parental care promotes the evolution of
725 sex differences in care and the ability to care. Proc R Soc Lond 282:20142752.
726 Meylan S, Miles DB, Clobert J, 2012. Hormonally mediated maternal effects, individual
727 strategy and global change. Philos Trans R Soc B 367:1647-1664. doi:
728 10.1098/rstb.2012.0020.
729 Moreno-Rueda G, 2007. Yolk androgen deposition as a female tactic to manipulate paternal
730 contribution. Behav Ecol 18:496-498. doi: 10.1093/beheco/arl106.
731 Moreno J, Lobato E, Morales J, Merino S, Tomás G, Martínez-de la Puente J, Sanz JJ, Mateo
732 R, Soler JJ, 2006a. Experimental evidence that egg color indicates female condition at
733 laying in a songbird. Behav Ecol.

734 Moreno J, Morales J, Lobato E, Merino S, Tomás G, Martínez-de la Puente J, 2006b. More
735 colourful eggs induce a higher relative paternal investment in the pied flycatcher
736 Ficedula hypoleuca: a cross-fostering experiment. J Avian Biol 37:555-560.
737 Moreno J, Osorno JL, 2003. Avian egg colour and sexual selection: does eggshell
738 pigmentation reflect female condition and genetic quality? Ecol Lett 6:803-806.
739 Mousseau TA, Fox CW, 1998. Maternal effects as adaptations. Oxford; UK: Oxford
740 University Press.
741 Müller W, Boonen S, Groothuis TGG, Eens M, 2010. Maternal yolk testosterone in canary
742 eggs: toward a better understanding of mechanisms and function. Behav Ecol 21:493-
743 500. doi: 10.1093/beheco/arq010.
744 Müller W, Lessells CM, Korsten P, von Engelhardt N, 2007. Manipulative signals in family
745 conflict? On the function of maternal yolk hormones in birds. Am Nat 169:E84-E96.
746 doi: 10.1086/511962.
747 Nijhout HF, 1998. Insect hormones: Princeton University Press.
748 Noguera JC, Kim S-Y, Velando A, 2013. Maternal testosterone influences a begging
749 component that makes fathers work harder in chick provisioning. Horm Behav 64:19-
750 25.
751 Paquet M, Covas R, Chastel O, Parenteau C, Doutrelant C, 2013. Maternal effects in relation
752 to helper presence in the cooperatively breeding sociable weaver. PLoS ONE
753 8:e59336. doi: 10.1371/journal.pone.0059336.
754 Paquet M, Covas R, Doutrelant C, 2015. A cross-fostering experiment reveals that prenatal
755 environment affects begging behaviour in a cooperative breeder. Anim Behav
756 102:251-258. doi: http://dx.doi.org/10.1016/j.anbehav.2015.01.034.

757 Quillfeldt P, Peter H-U, 2000. Provisioning and growth in chicks of Wilson's storm-petrels
758 (Oceanites oceanicus) on King George Island, South Shetland Islands. Polar Biology
759 23:817-824.
760 Requena GS, Buzatto BA, Munguia-Steyer R, Machado G, 2009. Efficiency of uniparental
761 male and female care against egg predators in two closely related syntopic
762 harvestmen. Anim Behav 78:1169-1176.
763 Ridley M, 1978. Paternal care. Anim Behav 26:904-932.
764 Rombough RJ, 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia
765 during early life. Fish physiol:59-161.
766 Royle NJ, Smiseth PT, Kölliker M, 2012. The evolution of parental care. Oxford: Oxford
767 Univ. Press.
768 Rubolini D, Romano M, Boncoraglio G, Ferrari RP, Martinelli R, Galeotti P, Fasola M, Saino
769 N, 2005. Effects of elevated egg corticosterone levels on behavior, growth, and
770 immunity of yellow-legged gull (Larus michahellis) chicks. Horm Behav 47:592-605.
771 Russell AF, Langmore NE, Cockburn A, Astheimer LB, Kilner RM, 2007. Reduced egg
772 investment can conceal helper effects in cooperatively breeding birds. Science
773 317:941-944. doi: 10.1126/science.1146037.
774 Ruuskanen S, Doligez B, Tschirren B, Pitala N, Gustafsson L, Groothuis TGG, Laaksonen T,
775 2009. Yolk androgens do not appear to mediate sexual conflict over parental
776 investment in the collared flycatcher Ficedula albicollis. Horm Behav 55:514-519. doi:
777 http://dx.doi.org/10.1016/j.yhbeh.2009.01.010.
778 Saino N, Bertacche V, Ferrari RP, Martinelli R, Moller AP, Stradi R, 2002. Carotenoid
779 concentration in barn swallow eggs is influenced by laying order, maternal infection
780 and paternal ornamentation. Proc R Soc Lond 269:1729-1733. doi:
781 10.1098/rspb.2002.2088.

782 Saino N, Romano M, Ferrari RP, Martinelli R, Moller AP, 2005. Stressed mothers lay eggs
783 with high corticosterone levels which produce low-quality offspring. J Exp Zool
784 Comp Exp Biol 303A:998-1006. doi: 10.1002/jez.a.224.
785 Sandell MI, Adkins-Regan E, Ketterson ED, 2007. Pre-breeding diet affects the allocation of
786 yolk hormones in zebra finches *Taeniopygia guttata*. J Avian Biol 38:284-290. doi:
787 10.1111/j.2007.0908-8857.03640.x.
788 Santos ESA, Macedo RH, 2011. Load Lightening in Southern Lapwings: Group-Living
789 Mothers Lay Smaller Eggs than Pair-Living Mothers. Ethology 117:547-555. doi:
790 10.1111/j.1439-0310.2011.01905.x.
791 Sanz JJ, García-Navas V, 2009. Eggshell pigmentation pattern in relation to breeding
792 performance of blue tits Cyanistes caeruleus. J Anim Ecol 78:31-41.
793 Savage JL, Russell AF, Johnstone RA, 2013. Intra-group relatedness affects parental and
794 helper investment rules in offspring care. Behav Ecol Sociobiol:1-11. doi:
795 10.1007/s00265-013-1595-5.
796 Savage JL, Russell AF, Johnstone RA, 2015. Maternal allocation in cooperative breeders:
797 should mothers match or compensate for expected helper contributions? Anim Behav
798 102:189-197.
799 Schwabl H, 1996. Maternal testosterone in the avian egg enhances postnatal growth. Comp
800 Biochem Phys A 114:271-276. doi: 10.1016/0300-9629(96)00009-6.
801 Schwagmeyer P, Mock DW, Parker GA, 2002. Biparental care in house sparrows: negotiation
802 or sealed bid? Behav Ecol 13:713-721.
803 Sheldon BC, 2000. Differential allocation: tests, mechanisms and implications. Trends Ecol
804 Evol 15:397-402. doi: 10.1016/S0169-5347(00)01953-4.

805 Smiseth PT, Amundsen T, Hansen LT, 1998. Do males and females differ in the feeding of
806 large and small siblings? An experiment with the bluethroat. Behav Ecol Sociobiol
807 42:321-328.
808 Smiseth PT, Moore AJ, 2004. Behavioral dynamics between caring males and females in a
809 beetle with facultative biparental care. Behav Ecol 15:621-628. doi:
810 10.1093/beheco/arh053.
811 Smiseth PT, Scott MP, Andrews C, 2011. Hormonal regulation of offspring begging and
812 mediation of parent-offspring conflict. Anim Behav 81:507-517. doi:
813 10.1016/j.anbehav.2010.11.029.
814 Smiseth PT, Kölliker M, Royle N, 2012. What is parental care? The evolution of parental
815 care:1-17.
816 Soler JJ, Moreno J, Avilés JM, MøLLER AP, Sorenson M, 2005. Blue and green egg-color
817 intensity is associated with parental effort and mating system in passerines: support for
818 the sexual selection hypothesis. Evolution 59:636-644.
819 Soler JJ, Navarro C, Contreras TP, Avilés JM, Cuervo JJ, 2008. Sexually selected egg
820 coloration in spotless starlings. The American Naturalist 171:183-194.
821 Stearns SC, 1992. The evolution of life histories: Oxford University Press Oxford.
822 Stoddard MC, Fayet AL, Kilner RM, Hinde CA, 2012. Egg speckling patterns do not
823 advertise offspring quality or influence male provisioning in great tits. PLoS ONE
824 7:e40211.
825 Taborsky B, 2006. Mothers determine offspring size in response to own juvenile growth
826 conditions. Biol Lett 2:225-228.
827 Taborsky B, Skubic E, Bruintjes R, 2007. Mothers adjust egg size to helper number in a
828 cooperatively breeding cichlid. Behav Ecol 18:652-657. doi: 10.1093/beheco/arm026.

829 Tallamy DW, 2001. Evolution of exclusive paternal care in arthropods. Annu Rev Entomol
830 46:139-165.
831 Thorogood R, Kilner R, Karadaş F, Ewen J, 2008. Spectral mouth colour of nestlings changes
832 with carotenoid availability. Funct Ecol 22:1044-1051.
833 Trivers RL, 1974. Parent-offspring conflict. Am Zool 14:249-264.
834 Trumbo ST, 2012. Patterns of parental care in invertebrates. The evolution of parental
835 care:81-100.
836 Tschirren B, Richner H, 2008. Differential effects of yolk hormones on maternal and paternal
837 contribution to parental care. Anim Behav 75:1989-1994. doi:
838 10.1016/j.anbehav.2008.01.007.
839 Underwood T, Sealy S, 2002. Adaptive significance of egg coloration. Oxford Ornithology
840 Series 13:280-298.
841 Vijendravarma RK, Narasimha S, Kawecki TJ, 2010. Effects of parental larval diet on egg
842 size and offspring traits in Drosophila. Biol Lett 6:238-241.
843 von Engelhardt, N., & Groothuis, T. G. G. (2011). Maternal hormones in avian
844 eggs. Hormones and reproduction of vertebrates: 91-127
845 von Schantz T, Bensch S, Grahn M, Hasselquist D, Wittzell H, 1999. Good genes, oxidative
846 stress and condition-dependent sexual signals. Proc R Soc Lond B 266:1-12.
847 Walters LA, Olszewski N, Sobol K, 2014. Male House Wrens provide more parental
848 provisioning to nests with a brighter artificial egg. Wilson J Ornithol 126:508-515.
849 Wright J, 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental
850 evidence from play-backs of chick begging. Behav Ecol Sociobiol 42:423-429. doi:
851 10.1007/s002650050456.
852 Wright J, Cuthill I, 1989. Manipulation of sex-differences in parental care. Behav Ecol
853 Sociobiol 25:171-181. doi: 10.1007/bf00302916.

854

Figure legends

Figure 1

A simple cost-benefit analysis for the optimal amount of male care. rB represents the benefit function of male care, defined as the effect of specific amount of male care on the offspring's fitness multiplied by the relatedness coefficient between the offspring and the male. C represents the cost function of male care, defined as the effect of specific amounts of male care on the male's ability to invest in other offspring. The optimal amount of male care to the male is the amount of care that provides the largest possible net benefit given rB and C, and is represented by M* and the vertical solid line. The optimal amount of male care to the female is represented by F* and the vertical dashed line. The conflict battleground is the difference in the optimal amount of male care between the two sexes and is represented by the horizontal double line.

Figure 2

Graphical representation of the two different forms of maternal manipulation: deception (a) and incentivization (b–c). Deception occurs when females bias the actual amount of care the male provides (M_a) away from the male's optimum (M*) and towards the female's own optimum (F*). Incentivization occurs when female increase male care by altering the shape of either the benefit function (b) or the cost function (c) of male care. Thus, with incentivization, the male still provides the optimal amount of care to the male, but this optimum has changed as a consequence of maternal effects on the benefits or the costs of care.

Figure 3

Illustration of potential causal pathways by which females may manipulate male parental effort via maternal effects that influence offspring traits. Pre-natal conditions, such as food availability and male parental quality, influence some maternal effects mechanism, such as deposition of androgens into the eggs. These maternal effects alter the offspring's phenotype by for example stimulating offspring begging, which in turn lead to an increase in male parental care. Ultimately, this increase in male parental care should enhance the fitness of the female and/or the offspring at the expense of the fitness of the male.

Table 1: Summary of the experiments and main results from the 6 previous studies that investigated the MAH.

Species	**Treatment**	**Effect on begging**	**Effect on male provisioning**	**Time begging measured**	**Time provisioning measured**	**Reference**
House wren *Troglodytes aedon*	T injected in eggs	+[a]	no	day 4-5 and 9-10	day 9-10	(Barnett et al., 2011)
Pied flycatcher *Ficedula hypoleuca*	cross fostering and 4^{rth}egg measured for T	NM	no	NM	day 5	(Laaksonen et al., 2011)
Collared Flycatcher *Ficedula albicollis*	T+A4 injected in eggs	NM	no	NM	day 9	(Ruuskanen et al., 2009)
Great tit *Parus major*	antiandrogen injection	NM	no[b]	NM	day 10	(Tschirren and Richner, 2008)
Canary *serinus canaria*	T injected in eggs	No	no	1 hour then daily for 10 days	day8-10	(Müller et al., 2010)
Yellow-legged Gull *Larus michaellis*	T injected in 3rd eggs	+	Yes?[c]	2 days	2 days	(Noguera et al., 2013)

NM: Not measured

[a]: Effect on begging at day 4-5 but not 9-10

[b]: In enlarged broods females feed more unmanipulated chicks

[c]: Positive relation between begging and male provisioning

1